

**LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF
XENOCHAETA DICHROMATA SNOW (DIPTERA: TEPHRITIDAE) ON
HIERACIUM ALBIFLORUM HOOKER IN CENTRAL AND
SOUTHERN CALIFORNIA**

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Abstract.—*Xenochaeta dichromata* Snow is a nearly monophagous, uni- or bivoltine, synovigenic, seed-feeding fruit fly attacking the flower heads of certain native hawkweeds (*Hieracium* spp., Asteraceae) in western North America. *Xenochaeta aurantiaca* (Doane) is synonymized with *X. dichromata*. The egg, first-third instar larvae, and puparium are described and all but the second instar are illustrated. The third instar is shagreened, i.e., meso-, metathorax, and abdominal segments are covered by minute, dome-shaped verrucae. *Xenochaeta dichromata* differs from other shagreened species in possessing a single row of verruciform sensilla circumscribing each thoracic and abdominal segment. The life cycle is of the aggregative type. Eggs are deposited singly in individual immature flower heads. Each larva consumes the entire contents of a single head, within which it overwinters as a prepuparium. Pupariation occurs in the spring and the newly emerged adults aggregate on the preblossom host plants to mate and oviposit. The possible use of this fly for biological control of hawkweeds in North America and abroad, e.g., in New Zealand, is discussed.

Key Words: Insecta, *Xenochaeta*, *Hieracium*, hawkweeds, biology, taxonomy of immature stages, florivory, monophagy, reproductive behavior, parasitoids, biological control of weeds

The rearing of a good series of females that key to *Xenochaeta aurantiaca* (Doane) and males that key to *X. dichromata* Snow from the same samples of mature flower heads of *Hieracium albiflorum* Hooker (Asteraceae) in southern California confirm that there is a single, sexually dimorphic species of *Xenochaeta*. These results provided us the opportunity to synonymize these tephritid species and to study the life history and describe the immature stages of this heretofore-little-known, nonfrugivorous fruit fly.

MATERIALS AND METHODS

Our field studies on *X. dichromata* focused mainly on laboratory dissections of

flower head samples collected in June or August from different locations on the western slopes of the Sierra Nevada Mountains in central and southern California during 1993–1995: (1) N of Union Valley Reservoir at 1700-m elevation, Eldorado National Forest, Eldorado Co., 19.ix.1993; (2) four sites between 1820 and 2050 m in Mountain Home State Forest, Tulare Co., 3–4.ix.1994; (3) S of Slate Mountain and E of Onion Meadow at 2120 m, Sequoia Nat. Forest (N-section), Tulare Co., 3.ix.1994; (4) S of Sampson Flat at 1210 m, Sequoia Nat. Forest (N-section), Fresno Co., 14.vi.1995. These locations were too far from Riverside to allow field observation of

adult behaviors. Samples of immature or mature flower heads of *H. albiflorum* were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Thirty eggs, five first-, 12 second-, and 18 third-instar larvae, and six puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional mature larvae and prepuparia were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. In 1994, those larvae and prepuparia not pupariating by mid-December were stored in a refrigerator at $2 \pm 1^\circ\text{C}$ until August, 1995, before returning them to humidity chambers. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in Hexamethyldisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, and studied with a JEOL JSM C-35 SEM in the Department of Nematology, University of California, Riverside.

Most adults reared from isolated puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cagings were used for longevity studies in the insectary of the Department of Entomology, University of California, Riverside, at $25 \pm 1^\circ\text{C}$, and 14/10 (L/D) photoperiod. Virgin male and female flies obtained from emergence vials were paired in clear-plastic petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1991, 1994) for direct observations, videorecording, and still-photography of their courtship and copulation behavior.

Plant names used in this paper follow Munz (1974); tephritid names and adult terminology follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Goeden et al. (1993, 1994a, b, 1995a, b) and Goeden and Teerink (1996a, b, c; 1997) and our earlier works cited therein. Means \pm SE are used throughout this paper. Voucher specimens of *X. dichromata* and its parasitoids reside in the research collections of RDG; preserved specimens of eggs, larvae and puparia are stored in a separate collection of immature Tephritidae maintained by JAT.

RESULTS AND DISCUSSION

TAXONOMY

Adult.—*Xenochaeta dichromata* and *X. aurantiaca* (Doane) were termed "rarely collected" tephritids by Foote et al. (1993). *Xenochaeta dichromata* was described from a single male (therefore holotype) by Snow (1894), and besides records for additional males, only a single female specimen has since been recorded (Foote and Blanc 1979, Foote et al. 1993). *Xenochaeta aurantiaca* was described (as a *Eutreta*) by Doane (1899) and only females heretofore were known. Noting these disparities in sexes recorded, Foote et al. (1993) suggested that "... further studies may show these two species to be conspecific." As predicted, only one, sexually dimorphic species is present in California, and these two names are synonyms. Both males of *X. dichromata* ($n = 34$) and females that keyed to *X. aurantiaca* ($n = 29$) were consistently and solely reared together from single samples of mature flower heads of *H. albiflorum* collected in August at the above-named study sites, and shortly after their pupariation and emergence as adults, these flies readily mated when placed together in petri dish arenas ($n = 5$, see below). Therefore, *X. aurantiaca* is hereby synonymized with *X. dichromata*, which has priority.

The wing patterns of both sexes of *X.*



Fig. 1. Egg of *X. dichromata*. pedicel to left.

dichromata were pictured in Foote et al. (1993), the female as *aurantiaca*, and the male wing pattern was figured in Foote and Blanc (1963).

Immature stages.—*Egg*.: Twenty eggs of *X. dichromata* were white, opaque, smooth; with an elongate-ellipsoidal body, 0.44 ± 0.002 (range, 0.41–0.46) mm long, 0.17 ± 0.002 (range, 0.17–0.19) mm wide, smoothly rounded at tapered posterior end, and with a peg-like anterior pedicel, 0.02 mm long (Fig. 1).

Third instar: Oblong-ovoid, tapering anteriorly, truncated posteriorly, shagreened (Fig. 2A); gnathocephalon conical, smooth, few rugose pads laterally (Fig. 2B); dorsal sensory organ a single, dome-shaped papilla (Fig. 2B-1, C-1); anterior sensory lobe (Fig. 2B-2, C) bears terminal sensory organ (Fig. 2C-2), pit sensory organ (Fig. 2C-3), lateral sensory organ (Fig. 2C-4) and supralateral sensory organ (Fig. 2C-5); stomal sense organ, a distinct lobe invested with sensoria ventrolaterad of anterior sensory lobe (Fig. 2B-3, D-1); mouth hooks tridentate (Fig. 2B-4, D-2); median oral lobe tapers anteriorly, attached to labial lobe (Fig. 2D-3); prothorax circumscribed anteriorly with minute acanthae, single row of verruciform sensilla circumscribe each thoracic and abdominal segment; anterior thoracic spiracles with 4–6 raised papillae (Fig. 2E); meso- and metathoracic lateral spiracular complexes consist of an open spiracle and

a single verruciform sensillum; abdominal lateral spiracular complexes consist of an open spiracle (Fig. 2F-1) and two verruciform sensilla (Fig. 2F-2); posterior spiracular plates consist of three ovoid rimae, ca. 0.03 mm in length (Fig. 2G-1), and four interspiracular processes, longest measuring 0.01 mm (Fig. 2G-2); verruciform sensilla circumscribe caudal segment (Fig. 2G-3); compound sensilla each consist of two verruciform sensilla, one with a central papilla (Fig. 2G-4, H).

Norrbom et al. (1997) placed *Xenochaeta* in the new Tribe Noectini along with *Acidogona* and *Jamesomyia*. Benjamin (1934) briefly described the immature stages of *Acidogona melanura* Loew, and the general habitus of the egg, mature larva, and puparium of this species do resemble *X. dichromata*. However, *X. dichromata* is the only species in the tribe for which the immature stages are described in detail.

Xenochaeta was placed in the Tribe Eutretini by Foote et al. (1993). Other genera and species in this tribe for which the immature stages have been described in similar detail include *Eutreta diana* (Osten Sacken) (Steck and Wharton 1986; Goeden 1990a, b) and *Paracantha gentilis* Hering (Headrick and Goeden 1990a). *Xenochaeta dichromata* differs from these two species in having a shagreened mature larva. Goeden (1990a) described *E. diana* (Osten Sacken) first instar as ringed with verrucae on abdominal segments II–V. However, the verrucae are absent or nearly so on the second and third instars (Steck and Wharton 1986, Goeden 1990a). Two species from other tribes in which the mature larva also are shagreened are *Tomoplagia cressoni* Aczel (Tribe Acrotaeniini) and *Valentibulla californica* (Coquillett) (Tribe Dithrycini) (Goeden and Headrick 1991, Goeden et al. 1995b, Foote et al. 1993). The latter of these two species most closely resembles *X. dichromata*, but lacks the verruciform sensilla that circumscribe the thoracic and abdominal segments in *X. dichromata*. Also, the posterior two-thirds of the prothorax is

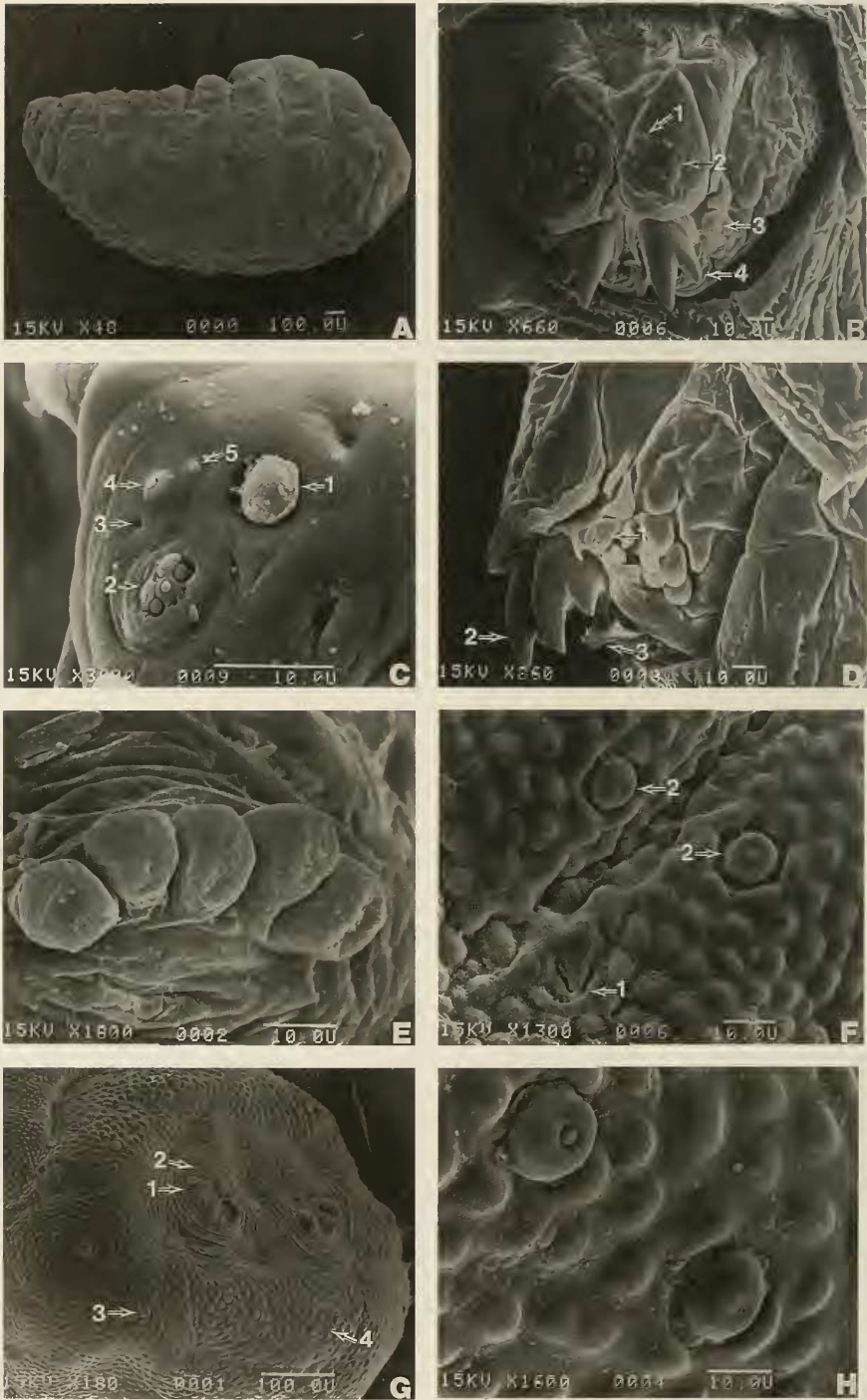


Fig. 2. Third instar of *X. dichromata*. (A) habitus, anterior to left; (B) gnathocephalon, anterior view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—stomal sense organ, 4—mouth hooks; (C) anterior sensory lobe, 1—dorsal sensory organ, 2—terminal sensory organ, 3—pit sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ; (D) gnathocephalon lateral view, 1—stomal sense organ, 2—mouth hooks, 3—median oral lobe; (E) anterior thoracic spiracle; (F) fourth abdominal lateral spiracular complex, 1—spiracle, 2—ver-



Fig. 3. First instar of *X. dichromata*. (A) habitus, anterior to left; (B) gnathocephalon, anterior view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—mouth hooks; (C) caudal segment, posterior spiracular plates.

shagreened in *V. californica*, the mouth hooks are bidentate, and the abdominal lateral spiracular complex consists of an open spiracle and a single sensillum (Goeden et al. 1995b).

Second instar: Elongate-ovoidal, rounded anteriorly and posteriorly, shagreened; gnathocephalon conical, few rugose pads laterad of stomal sense organ; dorsal sensory organ composed of a single papilla; anterior sensory lobe bears all four sensory organs; stomal sense organs distinct, ventrolaterad of anterior sensory lobe; mouth hooks bidentate; median oral lobe tapering anteriorly; thoracic segments smooth, single row of verruciform sensilla circumscribe thoracic and abdominal segments; anterior thoracic spiracles and lateral spiracular complex were not observed; posterior spiracular plates bear three ovoid rimae, ca. 0.018 mm in length and four interspiracular processes, longest measuring 0.006 mm; compound sensilla were not observed.

The second instar differs from the mature larva in that the dome-shape verrucae are smaller and restricted to the dorsad and intersegmental lines of the abdominal segments, and the mouth hooks are bidentate.

First instar: Elongate-ellipsoidal, minute verrucae circumscribing abdominal segments (Fig. 3A); gnathocephalon conical, smooth, lacking rugose pads (Fig. 3B); dorsal sensory organ consists of a dome-shaped papilla (Fig. 3B-1); anterior sensory lobe bears all four sensory organs (Fig. 3B-2); stomal sense organs indistinct; mouth hooks bidentate (Fig. 3B-3); median oral lobe not observed; prothorax with minute acanthae ventrally; posterior spiracular plates contiguous, bear two ovoid rimae and four interspiracular processes (Fig. 3C).

The first instar has fewer, smaller, dome-shaped verrucae than later instars. The first instar habitus is more ellipsoidal in shape,

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ruciform sensilla; (G) caudal segment, 1—rima, 2—interspiracular process, 3—verruciform sensillum, 4—compound sensillum; (H) posterior compound sensillum, verruciform sensillum with central papilla.

not as tapered anteriorly. Sensory structures such as the stomal sense organ are not as well-defined in the first instar as they are in the later instars. The verruciform sensilla circumscribing the thoracic and abdominal segments in the later instars were not observed.

Puparium: Dark brown, elongate-ellipsoidal, tapering anteriorly, rounded posteriorly, shagreened (Fig. 4A); anterior end bears invagination scar (Fig. 4B-1) and anterior thoracic spiracles (Fig. 4B-2); caudal segment bears posterior spiracular plates (Fig. 4C-1), compound sensilla (Fig. 4C-2), and verruciform sensilla (Fig. 4C-3). Twenty-five puparia of *X. dichromata* averaged 3.19 ± 0.05 (range, 2.85–3.60) mm in length; 1.61 ± 0.03 (range, 1.48–1.79) mm in width.

DISTRIBUTION AND HOSTS

The distribution of *X. dichromata* in North America north of Mexico was mapped by Foote et al. (1993) (also as *X. aurantiaca*) to include locations in British Columbia, California, Montana, Oregon, Utah, and Washington. Linda Wilson and J. McCaffrey (in litt. 1995, 1996) also have reared *X. dichromata* from *Hieracium albiflorum* and the *H. scouleri* Hooker complex in Idaho, but not from any of the introduced hawkweeds, e.g., *H. pratense* Tausch. Between 1987 and 1994, eight, 1-liter samples of mature flower heads of *H. albiflorum* collected by RDG (unpublished data) at locations in El Dorado, Fresno, Kern, Madera, Mono, and Trinity counties different from our above-named study sites all failed to yield *X. dichromata*. Similarly, six samples of mature flower heads of *H. horridum* Fries collected by RDG (unpublished data) from 1987–1993 yielded no *X. dichromata*. Only one other host-plant has been reported, *H. cynoglossoides* Arvet-Touvet (Novak et al. 1967, Foote et al. 1993), indicating that *X. dichromata* is nearly monophagous (one host genus) in flower heads of certain species of *Hieracium*, but does not occur in all parts of its



Fig. 4. Puparium of *X. dichromata*. (A) habitus, anterior to right; (B) anterior end, 1—invagination scar, 2—anterior thoracic spiracle; (C) caudal segment, 1—posterior spiracular plates, 2—compound sensilla, 3—verruciform sensillum.

host-plants' geographic ranges. Dodson and George (1986) demonstrated convincingly that the gall-forming tephritid flies *Acirina bigeloviae* (Cockerell) and *A. trixa* Curran

are less widely distributed than their host plants within four southwestern States.

BIOLOGY

Egg.—Only two (6%) of 34 preblossom flower heads contained two eggs each, the rest of these closed, immature heads each contained a single egg (Fig. 5A, B). Immature heads with eggs averaged 1.07 ± 0.04 (range, 0.64–1.50) mm in diameter. Eleven (32%) of 34 eggs examined were oriented with the long axis parallel to the long axes of the tiny, immature florets (Fig. 5A), 14 eggs (41%) were inserted nearly perpendicular to the long-axes (Fig. 5B) and nine eggs (26%) were inserted at angles of 45–60°. Only one (9%) of the 11 eggs inserted parallel to the florets (pedicel-last like all tephritid eggs examined by us to date, Fig. 5A), penetrated an ovule or floral tube; whereas 14 (60%) of the 23 eggs oviposited at an angle to the florets penetrated an ovule or floral tube after the aculeus had penetrated one or more phyllaries during oviposition. Ten eggs rested atop the immature florets and parallel to the receptacle in the small cavity formed by the overlapping phyllaries (Fig. 5B).

Larva.—Newly eclosed first instars (Fig. 5C) fed parallel to the receptacle on ovules or floral tubes inside closed heads that averaged 1.36 ± 0.08 (range, 1.14–1.71; $n = 7$) mm in diameter. Six first instars each damaged an average of 2.5 ± 0.7 (range, 1–5) florets. The second instar (Fig. 5D) fed centrally, well above and parallel to the receptacle, consuming the upper parts of the ovules and the bases of the floral tubes within a circle of intact, outer florets (Fig. 5D). Eleven feeding chambers of second instars within closed, immature, flower heads averaging 2.47 ± 0.14 (range, 1.71–3.13) mm in diameter measured 1.32 ± 0.12 (range, 0.85–1.71) mm by 1.03 ± 0.13 (range, 0.57–1.42) mm (Fig. 5D).

The third instar continued to enlarge the feeding chamber, eventually destroying all ovules and floral tubes within the infested heads (Fig. 5E, F). Thirty uninfested mature

heads of *H. albiflorum* produced an average of 19 ± 0.6 (range, 15–28) achenes. Usually, only one larva developed to maturity in each of 132 infested heads examined (Fig. 5E). Once the third instar consumed the florets, it deeply scored the receptacle and supplemented its diet with sap that collected in the feeding depression, as reported with several, but not all, florivorous, California Tephritidae that we have studied (Goeden 1988, Headrick and Goeden 1990a, b, Goeden and Headrick 1991, 1992, Goeden et al. 1993, 1995a, Headrick et al. 1996). The infested heads never opened or showed any protruding pappus apically and were more conical in shape than the ellipsoidal, uninfested heads (Fig. 5F). One hundred heads containing unparasitized mature larvae or prepuparia averaged 3.26 ± 0.05 (range, 2.00–4.57) mm in diameter (Fig. 5F). The feeding cavities of these fully grown, third instars measured 3.91 ± 0.05 (range, 1.71–5.13) mm in length by 2.23 ± 0.03 (range, 1.42–2.85) mm in width (Fig. 5E). The walls of these chambers were stiffened by a dried, hardened mixture of floret fragments, feces, and dried sap that coated and glued together the inner walls of the phyllaries (Fig. 5E).

Pupa.—Fully grown larvae ceased feeding, contracted their bodies, invaginated their mouthparts, and darkened ventrally and posteriorly to become prepuparia. Most prepuparia entered diapause and overwintered in the dried heads, but eight of 33 (25%) held in moist chambers in the laboratory in 1994 reversed their position 180° within excised flower heads, pupariated (Fig. 5G), and emerged as adults (Fig. 5H, I).

Adult.—Foote and Blanc (1979) remarked that the entire genus *Xenochaeta* at that time was represented in U.S. collections by a total of only 10–12 specimens. After 3 years of study, our reared specimens from California number 63, of which 34 (54%) are males. Adults were long-lived under insectary conditions, as 13 males averaged 48 ± 7 (range, 15–97) days, and 12

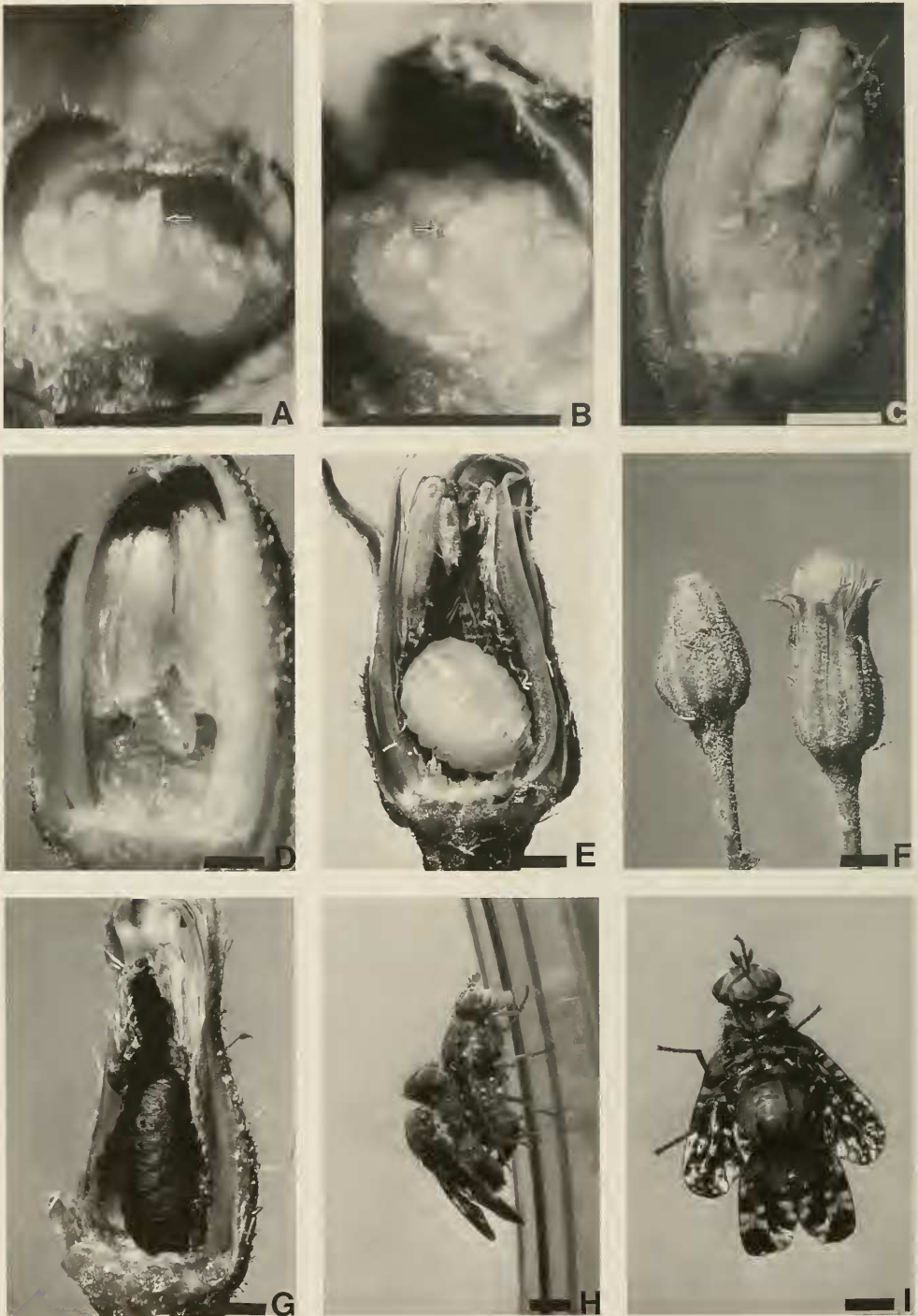


Fig. 5. Life stages of *X. dichromata* on *Hieracium albiflorum*. (A) egg (arrow) inserted between florets of immature, preblossom flower head; (B) egg (arrow) resting atop florets parallel to receptacle; (C) first instar feeding at base of floral tube; (D) second instar feeding on ovules and floral tube bases; (E) fully grown third instar in feeding chamber; (F) infested flower head containing third instar (left), uninfested head right; (G) Puparium in head; (H) mating pair, lateral view; (I) mating pair, ventral view. Lines = 1 mm.

females averaged 31 ± 5 (range, 8–65) days. Males ($n = 5$) readily mated when 3 to 18 days old; females ($n = 5$), when 3 to 17 days old (Fig. 5H, I). A 20-day-old female contained a full compliment of full-size ova, but otherwise ovigenesis and oviposition were not studied in the laboratory or field, nor were free-living adults ever observed or collected.

As observed with adults of *Eutreta diana* by Goeden (1990a, unpublished data) and *Paracantha gentilis* (Headrick and Goeden 1990a, 1995), adults characteristically rested or walked with their wings arched and parted and exhibited abdominal flexures. Another behavior exhibited by males of *X. dichromata* and *E. angusta* Banks (Headrick and Goeden 1995) was side-stepping displays by males when facing and tracking females in arenas. Wing displays by males and females of *X. dichromata* most commonly were synchronous supinations, and less commonly, slower paced, asynchronous wing supinations by males, or wing lofting of 20° embellished with rapid wing vibration, when tracking females. No abdominal pleural expansion by males was observed, and also unlike *P. gentilis* (Headrick and Goeden 1990a, 1995), initiation and termination of mating was simple and direct, involving little or no pre- or post-copulatory behaviors. Copulatory postures exhibited by both sexes were similar to those generally described for other nonfrugivorous tephritids (Fig. 5H, I). Five pairs mated 11 times on successive days for an average duration of 89 ± 14 (range, 22–145) min.

Seasonal history.—Like *Neaspilota viridescens* Quisenberry (Goeden and Headrick 1992), *Urophora timberlakei* Blanc and Foote (Goeden and Teerink 1995a), and other *Neaspilota* and *Urophora* spp. studied in southern California (our unpublished data), the life cycle of *X. dichromata* follows the aggregative pattern in which overwintering is largely by prepuparia in dead flower heads. These overwintered prepuparia pupariate and emerge as adults the

next spring or summer, or overwintering is by long-lived adults in reproductive diapause, that return to and aggregate on preblossom host plants during the following spring and summer to mate and reproduce (Headrick and Goeden 1995). It is also possible that adults of *X. dichromata* that emerge from flower heads in late summer (August) produce a second generation in late-forming, preblossom flower heads of *Hieracium albiflorum*, or different, as yet undetermined, alternate host plant(s), at higher elevations (Goeden and Headrick 1992; Goeden et al. 1995a).

Natural enemies.—Two species of solitary, hymenopterous, parasitoids were reared from puparia of *X. dichromata* in flower heads of *H. albiflorum* and were identified for us as *Pteromalus* sp. (Pteromalidae) and Braconinae sp. (Braconidae). The former species was the more common parasitoid.

Biological control.—In the northwestern United States, three species of *Hieracium* native to Eurasia are weeds of forests, pastures, meadows, and wetlands: mouseear hawkweed (*H. pilosella* L.), orange hawkweed (*H. aurantiacum* L.), and yellow hawkweed (*H. pratense* Tausch). In addition, two weedy native species, narrowleaf hawkweed (*H. umbellatum* L.) and Canadian hawkweed (*H. canadense* Michaux) are found in the Northwest (Birdsall and Quimby 1996). In New Zealand, four introduced species of European origins (including *H. pilosella*) are invasive weeds affecting livestock production and native-plant and soil conservation in grasslands (Syrett and Sárosataki 1993). Holm et al. (1979) listed Canada, Russia, and Finland as additional countries in which hawkweeds are problems. A consortium reportedly has been formed to identify and assess candidate agents for biological control of hawkweeds. This group includes representatives from the U.S. Department of Agriculture, Agricultural Research Service; University of Idaho; Agriculture Canada; the International Institute of Biological Control, Swit-

zerland and United Kingdom; the Commonwealth Scientific and Industrial Research Organization, Australia; and Landcare Research New Zealand Limited (Birdsall and Quimby 1996). The final draft of the present report was given to colleagues representing selected member organizations in this consortium for their possible interest in *X. dichromata* as a candidate biological control agent, especially for export to New Zealand, if it will attack and reproduce on one or more of the weedy species introduced there. As noted above, this nearly monophagous fruit fly attacks only some native North American species of *Hieracium*, and apparently, has not been reared from any introduced weedy species. Consequently, it may prove too host specific for domestic redistribution and augmentation, or otherwise unsuitable for export, like other native North American insects found attacking native and introduced weeds (cf., Goeden and Kok 1986, Goeden and Teerink 1993, Goeden and Palmer 1995).

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